

LARVAL DESCRIPTION OF A NEW WORLD GHOST MOTH, *PHASSUS* SP.,
AND THE EVOLUTIONARY BIOGEOGRAPHY OF WOOD-BORING
HEPIALIDAE (LEPIDOPTERA: EXOPORIA: HEPIALOIDEA)

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Abstract.—We present a description of chaetotaxy and selected morphological features for an unidentified *Phassus* larva and examine the implications for hepialoid chaetotaxy and biogeography. The wood-boring genera *Phassus*, *Endochlita*, and *Aenetus* represent a monophyletic lineage in reference to the presence of a microtrichiated field enclosing SD1, SD2 and D2. Other larval characters that may support this clade include a longitudinal pit posteroventral to L1 on the meso- and metathorax, and a medial triangular tooth on the labral margin. The wood-boring *Zelotypia* and *Cibyra* may represent more distant relatives within a monophyletic lineage of callus feeders and wood-borers within the Hepialidae sensu stricto. The spatial and nomenclatural problems in Lepidoptera chaetotaxy are reviewed with respect to *Phassus*. The term “microtrichiated pit” is distinguished from “microtrichiated field” referring to an extensive, concave or flat region that may enclose one or more setae. We argue that slight shifts in setal position and tonosensillar morphology for SD2 of the prothorax is more likely than convergent development of tonosensillar morphology in D2. A monophyletic relationship between *Phassus*, *Endochlita*, and *Aenetus* is biogeographically congruent with a Pacific basin origin rather than a typically ‘Gondwanic’ history. We suggest that much of the biogeography and evolution of the Hepialidae is closely associated with Pacific geology and tectonics and this would be consistent with what otherwise would be an “extraordinary and inexplicable” absence of Exoporia from parts of West Africa and Madagascar.

Key Words: Hepialidae, larva, chaetotaxy, biogeography, panbiogeography, *Phassus*

The Hepialidae (Lepidoptera: Suborder Exoporia) is almost global in distribution comprising 616 described species placed in 68 genera (Nielsen et al. 2000). Phylogenetic relationships within the Hepialidae are poorly understood with most studies focusing on the establishment and composition of genera and subgenera (e.g., Tindale 1932–1942, Viette 1946–1979, Nielsen and Robinson 1983, Dugdale 1994). The genera *Afrotheora* Nielsen and Scoble, *Antihepi-*

alus Janse, *Fraus* Walker, and *Gazoryctra* Hübner lack derived features of other hepialids and comprise a basal group of uncertain monophyly (Nielsen and Kristensen 1989, Kristensen 1998). The remaining genera constitute the great majority of species and are believed to represent a monophyletic assemblage, the Hepialidae sensu stricto (Kristensen 1998).

Recent studies by Nielsen and Robinson (1983) and Nielsen and Kristensen (1989)

attempted preliminary phylogenetic analysis of species relationships within selected genera, but intergeneric relationships remain generally uncertain. Wagner and Rosovsky (1991) examined the relationships of ten genera (nine restricted to North America and Eurasia) where male courtship behavior was known, and an unpublished revision by Wagner (1985) hypothesized a monophyletic status for *Phymatopus* from western North America and Eurasia. A morphological study by Brown et al. (2000) presented a cladistic phylogeny for the New Zealand Hepialidae, and Nielsen et al. (2000) catalogued the entire Hepialidae within an informal speculative phylogenetic arrangement.

Most hepialid larvae, including all the basal lineages, live in soil and feed on or within roots, or consume leaves and other herbaceous debris, including mosses and both monocotyledonous and dicotyledonous angiosperms. Host-plant relationships dissociated from soil microhabitats evolved in the genera *Aenetus* Herrich-Schäffer, *Cibyra* Walker (= *Aepytus* Herrich-Schäffer), *Endoclyta* Felder, *Phassus* Walker, *Trichophassus* Le Cerf, and *Zelotypia* Scott where larvae enter the host-plant above ground level and tunnel into stems and branches. Larvae of *Endoclyta*, *Trichophassus*, and *Zelotypia* are known to feed on callus tissues forming around the tunnel entrance (Rojas de Hernández and Chacón de Ulloa 1982, Grehan 1987, Grehan 1989). The primary food source for *Cibyra* remains unconfirmed (Rojas de Hernández and Chacón de Ulloa 1982, Hilje et al. 1992). Stem boring is documented for the monotypic genus *Leto* Hübner (Janse 1939, Duke and Taylor 1964) although whether larval activity originates within stems or is an extension of root-feeding is unknown. Fragments of the host-plant with tunnels (Peabody Museum of Natural History) do not show evidence of callus feeding.

By applying Hennig's vicariance criterion (Craw et al. 1999), Grehan (1987) predicted that the *Endoclyta* lineage was most

closely related to *Aenetus/Zelotypia* through vicariant differentiation of a widespread ancestor. Morphological characters subsequently identified in support of this lineage include the shared presence of sub-falcate forewings, reduced adult antennae, a weak truelum in the male genitalia, a small ventral spine crest on the seventh abdominal segment of pupae, and a prothoracic depression (or field) enclosing setae SD1, SD2, and D2 in larvae (Dugdale 1994). Absence of this trisetose feature in primitive *Fraus* and the hepialoid sister group Mnesarchaeidae led Nielsen and Kristensen (1989) to suggest it represented an apomorphy within Hepialidae.

Kristensen (1999) suggested male metatibial androconial scales may support a monophyletic lineage within Hepialidae sensu stricto (Table 1), including the callus-feeding genera *Aenetus*, *Endoclyta*, and *Zelotypia*. These genera are exclusively wood-borers. Of the remaining androconial genera, only the Mexican-South American *Phassus* is known as a wood-borer (Grehan 1989). Root and stem boring is reported for the *Phymatopus*-clade of Wagner (1985), while larvae of *Sthenopus* Packard and related *Zenophassus* Tindale feed from roots into stems, although neither is reported feeding on callus (Grehan 1989). Larvae of *Oncopera* Walker feed on leaves of grasses and other herbaceous perennials (Grehan 1989), but the feeding biology of monotypic *Puermytrans* Viette is unknown (Nielsen and Robinson 1983).

The specialized trisetose prothoracic field represents a potential larval apomorphy for callus-feeding wood borers. Detailed larval descriptions of wood-boring larvae are limited to *Aenetus cohici* Viette (Boudinot 1991) *Aenetus virescens* (Herrich-Schäffer) (Grehan 1981, Dugdale 1994) and *Endoclyta hosei* Tindale (Yasuda and Abe 1986). Larvae of other wood-boring genera are undescribed, or have received only generalized treatment. Larval descriptions of American wood-borers are limited to a general account of *Trichophassus giganteus* Le

Table 1. Feeding modes, geographical distributions, and important morphological features of ghost moth genera (Hepialidae). ? = character not recorded; * = inferred by probable relationship of *Zenophasstus* with *Sithenopsis*.

Genus	Feeding Mode	Geographic Range	Androconia Present	Androconia Red-Brown	Trisetose Thoracic Pit	Trilobate Labrum
<i>Puermytrans</i>	?	South America	yes	no	no	?
<i>Oncopera</i>	foliage	Australia	yes	no	no	no
<i>Sithenopsis</i>	root/stem	America/Eurasia	yes	yes	no	yes
<i>Zenophasstus</i>	root/stem	Europe	yes	yes	?*	?*
<i>Phymatopus</i>	root	Europe	yes	yes	yes	?
' <i>Phymatopus</i> '	root/stem	Northwestern North America	yes	yes	yes	yes
<i>Schausiana</i>	?	Mexico	yes	yes	?	?
<i>Phassus</i>	stem	America	yes	yes	yes	yes
<i>Aenetus</i>	stem	Southwest Pacific	yes	yes	yes	yes
<i>Endoclita</i>	stem	India/Asia	yes	yes	yes	yes
<i>Zelotypia</i>	stem	Australia	no	no	no	yes
<i>Trichophasstus</i>	stem	Brazil	no	no	?	?
<i>Cibyra (Aepytus)</i>	stem	South America	no	no	no	?
<i>Leto</i>	stem	South Africa	no	no	no	yes

Cerf by Briquelot (1956) and brief notes on *Phassus triangularis* Henry Edwards (Schaus 1888, Dyar 1917). A color photograph of an unidentified *Phassus* larva from Ecuador by Gara and Onore (1989) indicates a shaded area corresponding to a prothoracic sensory field. In this paper we describe the larva of an undetermined species of *Phassus*, confirm the presence of a prothoracic field, and discuss phylogenetic and biogeographic implications of this character for the evolutionary history of wood-boring Hepialidae.

METHODS

Specimens examined.—One dried larva from Jalapa, Mexico (No. 15646, Collection of Henry Edwards, American Museum of Natural History (AMNH)), and four ethanol-preserved specimens (National Museum of Natural History, Smithsonian Institution (USNM)) found boring in living stems of *Lantana camara* Linnaeus by N. H. L. Kraus, as follows: one from Nogales, Veracruz, Mexico and one from Orizaba, Veracruz, Mexico, both during December, 1954; one from Orizaba, Veracruz, Mexico (Kraus 5053), and one from Cordoba, Veracruz, Mexico (Kraus 5055), both in No-

vember, 1954. The chaetotaxy of *Phassus* sp. was compared with specimens or descriptions of about 34 species of Hepialidae and one species of Mnesarchaeidae (Table 2).

The following description is based on study of the above larvae that did not differ significantly in morphology. Measurements are given only for the single, most intact larva (Orizaba, Mexico, December, 1954). All are ultimate or penultimate instars based on head width and body size.

Although the specimen from Jalapa (AMNH) and the two from December, 1954 (USNM) were determined as *Phassus argentiferus* Walker by the collectors, only the generic determination can be accepted with confidence. No reared adult material is associated with these larvae, but they are most likely *Phassus* as indicated by distribution and morphology. Three genera of Hepialidae are known as adults from Mexico (*Phassus* Walker with more than 8 species in Mexico, monotypic *Schausiana* Viette, and *Cibyra* Walker (sensu Nielsen et al. 2000), the latter containing a few Mexican species formerly placed in *Hampsoniella* Viette, *Pseudodalava* Viette, and *Gymeloxes* Viette, all currently treated as subgenera of *Cibyra*. We expect larvae of the

Table 2. Taxa of Hepialidae and Mnesarchaeidae with larval material included in this study. Larval specimens were examined directly (with specimen depository) or cited from published descriptions. (with reference citation).

Name	Location	Instar	Depository/Source
<i>Abantiades latipennis</i> Tindale, 1932	Australia: Tasmania	late-final	Forestry Tasmania, Department of Primary Industries
<i>Aenictus cobici</i> Viette, 1961	New Caledonia: Mt. Kocamonoa	late-final	John Grehan Collection
<i>Aenictus dulcis</i> (Swinhoe, 1892)	Australia: Western Australia	late-final	John Grehan Collection
<i>Aenictus virescens</i> (Doubladay, 1843)	New Zealand: North Island	late-final	John Grehan Collection
<i>Aenictus cf. scotti</i> (Scott, 1869)	Australia: Victoria	late-final	John Grehan Collection
<i>Anthipellus</i> sp.	South Africa: Storm River	post-first	John Grehan Collection
<i>Aorata insularis</i> Dugdale, 1994	New Zealand: South Island	final	Dugdale (1994)
<i>Cibyra sarta</i> (Schaus, 1894)	Colombia	post-first	Rojas de Hernandez and Chacón de Ulloa (1980)
<i>Cladocycanus minus</i> (Hudson, 1905)	New Zealand	final	Dugdale (1994)
<i>Dalaca</i> sp.	Costa Rica: Santa Rosa	post-first	Illinois Natural History Survey
<i>Dioxycanus faxa</i> (Philpott, 1914)	New Zealand	final	Dugdale (1994)
<i>Dumbletonius charactertifer</i> (Walker, 1865)	New Zealand	final	Dugdale (1994)
<i>Dumbletonius unimaculata</i> (Salmon, 1948)	New Zealand: Kapiti Island	final	John Grehan Collection
<i>Elhamma</i> sp.	Australia: Eastwood	late-final	Peabody Museum of Natural History
<i>Endocleita exvrescens</i> (Butler, 1877)	Japan: Kyushu	late-final	Landcare, New Zealand
<i>Endocleita sinensis</i> (Moore, 1877)	Japan: Kyushu	late-final	Landcare, New Zealand
<i>Fraus simulans</i> Walker, 1856	Australia	late-final	Peabody Museum of Natural History
<i>Hepialus humali</i> (Linnaeus, 1758)	England	final	Aitkenhead and Baker (1964)
<i>Korscheltellus gracilis</i> (Grote, [1865])	United States: Vermont	final	John Grehan Collection
<i>Korscheltellus lupulina</i> (Linnaeus, 1758)	England	final	Aitkenhead and Baker (1964)
<i>Leto venus</i> (Cramer, 1780)	South Africa: Plattenburg Bay	late-final	South African Museum, Cape Town
<i>Mnesarchaea acuta</i> Philpott, 1929	New Zealand: Waitutuomata	late-final	George W. Gibbs Collection
<i>Oncopera fasciculatus</i> (Walker, 1869)	Australia: Kalangadoo	late-final	Peabody Museum of Natural History
<i>Oncopera intricata</i> Walker, 1856	Australia: Tasmania	late-final	Peabody Museum of Natural History
<i>Oncopera rufobrunea</i> Tindale, 1933	Australia: Tasmania	late-final	Peabody Museum of Natural History
<i>Oxyacanthus antipoda</i> (Herrich-Schäffner, [1853])	Australia: Tasmania	late-final	Peabody Museum of Natural History
<i>Pharmacis aemiliana</i> (Constantini, 1911)	Italy	final	Zalli (1998)
<i>Pharmacis fuscobalbalosa</i> (De Geer, 1778)	England	final	Aitkenhead and Baker (1964)
<i>Phaesus</i> sp.	Mexico: Jalapa, Veracruz	late-final	Smithsonian Institution
<i>Phymatoptus californicus</i> (Boisduval, 1868)	United States: California	late-final	John Grehan Collection
<i>Phymatoptus hecta</i> (Linnaeus, 1758)	England	late-final	John Grehan Collection
<i>Sthenopsis argenteomaculatus</i> (Harris, 1841)	United States: Vermont	late-final	John Grehan Collection
<i>Sthenopsis purpurascens</i> (Packard, 1863)	Canada: Quebec	late-final	Canadian National Collection
<i>Triodia sylvina</i> (Linnaeus, 1761)	England	final	Aitkenhead and Baker (1964)
<i>Wixania cervinata</i> (Walker, 1865)	New Zealand	final	Dugdale (1994)
<i>Zelotypia staceyi</i> Scott, 1869	Australia: New South Wales	final	Peabody Museum of Natural History

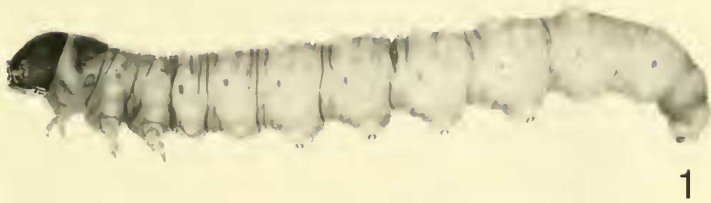


Fig. 1. Photograph of preserved last larval instar of *Phassus*, unidentified species.

Cibyra alliance to lack a prothoracic microtrichiated field enclosing macrosetae SD1, SD2, and D2 based on the larval description of *Cibyra sertis* (Schaus) (Rojas de Hernández and Chacón de Ulloa 1982).

Two larvae (from Nogales (USNM) and Jalapa (AMNH)) were macerated in warm 10% aqueous potassium hydroxide and soft tissues removed. The head capsule was removed by an incision along the posterior margin. The thoracic and abdominal cuticle was flattened under a glass slide for examination and subsequently stored in 70% ethanol.

Terminology.—At the present time the larval chaetotaxy of Hepialidae is a confusing patchwork of prior systems of nomenclature dating from Hinton (1946) and Gerasimov (1952). The terminology used in this paper follows in large part the general practice of recent authors (e.g., Nielsen and Kristensen 1989, Dugdale 1994, Zilli 1998) and makes no attempt to resolve homology issues with non-exoporian taxa. The chaetotaxy of the head capsule used here differs from that of Hinton (1946), following with few exceptions the nomenclature of Hasenfuss (1969) as a better-supported homology arrangement corresponding to ditrysian chaetotaxy (Leonard et al. 1992). Labeling of prothoracic setae SD1, SD2 and D2 follows Wagner (1987) and Wagner et al. (1989). For consistency, nomenclature of other setae and pores follow recent descriptive work on larval hepialids (Nielsen and

Kristensen 1989) with any deviations noted in the text. Chaetotaxy is illustrated by a semischematic setal map for thoracic abdominal segments (T1–A2 and A6–A10, Fig. 4–5). Lengths of setae are given in general terms relative to a large, precisely measured seta on most segments.

DESCRIPTION

Last instar (Fig. 1).—Exoporian, hepialoid, hepialid (Nielsen and Kristensen 1989). Length, 56 mm; maximum head width, 5.84 mm; head length from epicranial notch to apex of frontoclypeus, 4.88 mm. Head weakly hypognathous, subspherical, maximum width slightly less than prothorax but greater than other segments. Body elongate, parallel-sided, narrowing from Ab8 to Ab10; Ab8 slightly gibbose dorsally, longer than other segments except Ab7; setae short, inconspicuous, set in large flattened pinacula or plates paler than adjacent cuticle; cuticle of body between sclerotized plates and pinacula densely shagreened with fine microtrichiae. Prolegs present on Ab3 to Ab6, subequal to each other, smaller than prolegs on Ab10.

Color: Head dark reddish brown, body paler grayish red brown except for pale yellow to brownish-yellow pinacula, these prominent as pale transverse dorsal folds on Ab1 to Ab8; prothoracic dorsal shield reddish brown, edged anteriorly and ventrally with brownish yellow; ventral areas colorous with non-sclerotized areas on rest

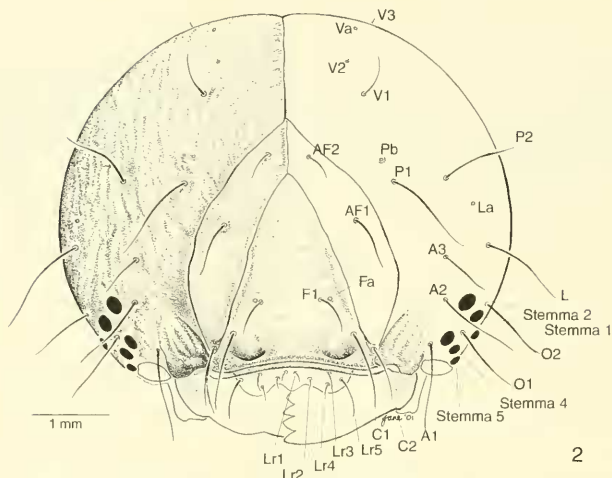


Fig. 2. Chaetotaxy of head of last instar larva of *Phassus* sp., Veracruz, Mexico; dorsofrontal view of head capsule. Symbols used: A1–A3, anterior setae; Aa, anterior pore; AF1–AF2, adfrontal setae; C1–C2, clypeal setae; F1, frontal seta; Fa, frontal pore; L1, lateral seta; La, lateral pore; Lr1–Lr5, labral setae; V1–V3, vertexal setae; Va, vertexal pore; G1, genal seta; P1–P2, posterior setae; Pb, posterior pore; O1–O2, ocular or stemmatal setae; Sb, stemmatal pore; SO2–SO3, subocular or substemmatal setae.

of body; prolegs paler, contrasting with ventral abdominal coloration. Setae brown, spiracles black.

Head (Figs. 2–3): Epicranium subspherical, circular in dorsal view, smooth; post-occipital sclerites and sutures as in other Hepialidae; epicranial notch obscure; coronal suture (= epicranial suture from epicranial notch to ecdysial lines) about twice length of epicranial suture from ecdysial lines to dorsal apex of front. Front fused to clypeus with frontoclypeal suture obsolete, anterior clypeal region with a large, sclerotized protuberance on each side. Six stemmata on each side in two dorsoventral arcs, anterior arc of stemmata 3, 4, and 5 (dorsal to ventral), posterior arc of stemmata 2, 1, and 6 (dorsal to ventral); stemma 5 not displaced ventrally into paramaxillary region; distinct pore anteroventral of stemma 4. Antennal fossa closed ventrally by pre-antennal bar that articulates with epicranium anterior to antenna and is posterior (not

contiguous) to dorsal mandibular articulation. Antennal slit (sensu Dugdale 1994) a narrow strip of membranous cuticle continuous with that between antenna and base of mandible, extending posterodorsad and ending near two distinct pores just ventral to stemma 5. Antenna not studied.

Setation of head as for other Hepialidae (Nielsen and Kristensen 1989). Dugdale (1994) following nomenclature of Hasenfuss (1969) although homology of that system with ditrysian nomenclature (e.g., Stehr 1987) doubtful. Seta V1 macrosetose, setae V2 and V3 microsetose; pore present near seta P1 (termed Pb by Nielsen and Kristensen 1989); pore La present; pore medial to seta SO1 visible only in ventral view (perhaps homologous with pore S5a of ditrysian system); pores Sa (= Oa of Hasenfuss 1969), MGA, AFA, and Aa absent; two genal microsetae; seta SO3 minute, microsetose (not visible or depicted in Fig. 3).

Labrum with five pairs of setae; anterior

margin with medial, broadly triangular tooth. Maxillolabial complex with basistipes and dististipes sclerotized. Maxillary palp three-segmented with distal segment subequal in size to large sensillum basiconicum as in other Hepialidae; lateral pore on basal segment of palp. Medial maxillary lobe laterally sclerotized with seven sensilla on distal surface; three large flattened sensilla dorsally, middle row of two apically rounded sensilla, lower row of two pointed sensilla with pitlike structure between them. Basistipes with two setae and a pore. Dististipes with single lateral seta. Labial palp minute with long apical seta, arising from lateral subapical plates of premental lobe (maxillary features similar to those illustrated for *Fraus* (Nielsen and Kristensen 1989)). Mandible with four triangular teeth on distal extremity; oral surface of mandible transversely rugulose without distinct molar area; mandible with two setae on aboral surface, basal seta M1, distal M2.

Prothorax (Fig. 4): Entire dorsal surface of prothorax sclerotized, anterior margin reflexed to join posterior margin of head capsule; prothoracic dorsal shield (sensu stricto) thicker and indistinctly delimited from sclerotized marginal regions, yellowish brown; sclerotization of dorsal shield includes L-group setae, narrowly separated from sclerotized region around spiracular peritreme.

Seta D1 strong, posterior to anterior margin of dorsal shield at a distance subequal to length of seta (0.76 mm); seta XD1 directly ventral to seta D1, more than twice as long. Seta XD2 slightly anterior to XD1, subequal in length to D1; seta D2 slightly ventral to level of XD2, slightly smaller than D1, approximately midway between SD1 and SD2. Three prothoracic pores (sensu Nielsen and Kristensen 1989): XDa directly ventral to D1, pigmented dark brown; XDb posterodorsal to XD1, pale; XDc posterodorsal to XD2, strongly pigmented; diameter of all pores slightly less than socket of associated setae.

Seta D2 ventral and slightly anterior to

seta SD2, dorsal and slightly posterior to seta SD1; length of seta D2 0.59 mm; length of SD1 0.42 mm, equal to SD2. Both SD setae extremely slender, filiform, not attenuate, arising from bottom of distinct conical pits with strongly microtrichiated walls (similar to tonosensilla of ditrysian larvae); cuticular articulation of D2 unmodified with setal alveolus (socket) surrounding visible, pale setal membrane bearing base of seta. Seta D2, both SD setae, and associated pits included within broad region (field) depressed below surrounding cuticle (Fig. 6), continuously microtrichiated (shagreened) more densely than adjacent cuticle or elsewhere on body; basal pits of setae SD1 and SD2, and base of seta D2, darkly pigmented, contrasting with microtrichiated field; maximum dorsoventral dimension of microtrichiated field 1.45 mm, width 0.55 mm. Small unnamed pore on extreme dorsal edge of microtrichiated field dorsal to a line between setae D1 and SD2, diameter smaller than alveolus of seta D2, but greater than diameter of hyaline setal membrane at bases of SD1 and SD2.

Seta L1 near anterior edge of prothoracic shield directly anterior to middle of spiracle, subequal in length to seta XD1. Seta L2 anterodorsal to seta L1, approximately half the length of seta L1. Seta L3 directly anterior to middle of spiracle, displaced from anterior peritreme by less than horizontal diameter of spiracle, shortest seta on prothoracic shield (half the length of seta L2). Setae SV1 and SV2 below L-group setae on pinaculum narrowly separated from ventral edge of prothoracic shield; SV1 subequal in length to XD2 or D1, directly posterior to seta SV2 and twice its basal diameter; SV pinaculum yellowish tan, concolorous with ventral lobe of prothoracic shield.

Seta V1 subequal in size to seta L3, posterior to prothoracic coxae on sclerotized mid-ventral plate. Seta MV3 macrosetose, subequal in size to seta L2, directly anterior to coxa; seta V1 on large plate which crosses ventral midline; seta MV2 macrosetose,

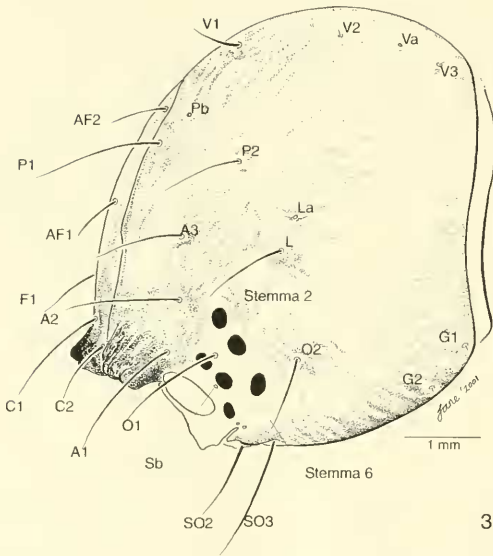


Fig. 3. Chaetotaxy of head of last instar larva of *Phassitis* sp., Veracruz, Mexico; lateral view of head capsule. Symbols used as in Fig. 2.

subequal in size to seta V1, anterior to middle of prothoracic coxa on extreme anterior edge of cuticular fold such that seta is appressed to head capsule midway between cranial setae G1 and G2.

Spiracle vertically ovate, 0.89 mm high, 0.35 mm long; outer peritreme heavily sclerotized, darkly pigmented; inner (filter) recessed into atrium approximately 0.10 mm.

Prothoracic leg (Figs. 7–8): Prothoracic coxae proximate at base across ventral midline. Coxa with eight setae: anterodorsal pair (Cx1, Cx2) very small, subequal in size, near proximal edge of coxa with Cx1 dorsalmost; anteroventral setal pair (Cx3, Cx4) unequal in size with anterior Cx3 as small as Cx1 and posterior Cx4 longer and thicker; posteroventral setal pair (Cx5, Cx6) with Cx5 longest and most ventral; Cx6 near middle of posteroventral expanse of coxa, slightly shorter than Cx5; posterodor-

sal pair (Cx7, Cx8) subequal to Cx1; Cx7 near proximal edge of coxa and dorsalmost; Cx8 near upper middle of posterodorsal swelling of coxa. Trochanteral seta Tr1 microsetose, in extreme dorsal portion of trochanterofemoral membrane on anterior surface of leg; trochanteral pore Tra close by [second trochanteral pore Trb of Nielsen and Kristensen (1989) not evident]; trochanteral seta Tr2 microsetose, in trochanteral membrane at ventral (adaxial) edge of leg; trochanteral seta Tr3 microsetose, in extreme dorsal portion of trochanterofemoral membrane on posterior surface of leg. Femoral seta Fe1 the largest and longest seta on legs, midlength on ventral edge of femur; femoral seta Fe2 near distal posteroventral edge of femur. Six tibial setae [nomenclature as Nielsen and Kristensen (1989)], all in distal half of tibia; Ti1, Ti3, and Ti5 on anterior surface of tibia, dorsal, subventral, and ventral respectively; Ti2,

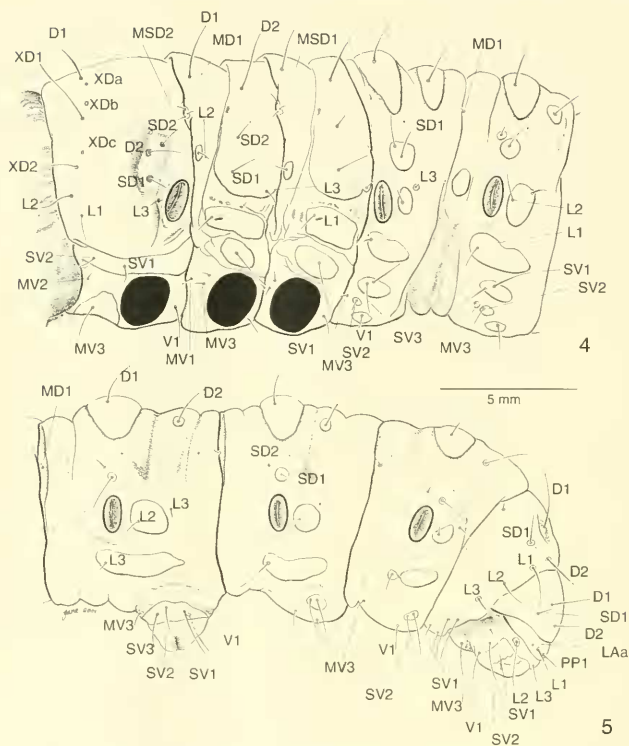
Ti4, and Ti6 on posterior surface of tibia, dorsal, subventral, and ventral respectively; tibial pore Tia conspicuous, in posterodorsal surface of tibia near midlength. Four tarsal setae; dorsal pair near distal end of tarsus, Ta1 anterior, Ta2 posterior; ventral pair unmodified in shape, on ventral edge of tarsus, Ta3 at distal extremity, Ta4 directly basal to Ta3 near midlength of tarsus, shorter and thinner than Ta4. Tarsal claw smoothly tapered with slight ventral impression near base; without teeth or other modifications.

Mesothorax (Fig. 4): Two transverse dorsal shields continuously fused across dorsal midline; anterior mesothoracic shield bearing seta D1 (0.76 mm in length, subequal in size to D1 on prothorax), extending ventrad to level of seta XD2 on prothorax; D1 directly posterior to seta XD1 of prothorax. Posterior mesothoracic shield with seta D2 nearly twice the size of seta D1 (length 1.37 mm, subequal to seta D2 on prothorax), directly ventral to seta SD2, posterior to D1, and directly posterior to prothoracic seta SD1; posterior mesothoracic shield pale yellow with seta L3 in posteroventral corner; L3 very small, subequal to L3 on prothorax. Seta L1 on anterior end of distinct lateral shield; longitudinal pit posteroventral to L1, brown, sclerotized. Seta L2 subequal in size to L3, on fold directly below ventral extremity of anterior mesothoracic shield and directly anterior to SD1. Setae MD1, MSD1, and MSD2 located on surface of a single lateral fold which is occluded from view by posterior lobe of prothorax and bulging anterior shield of mesothorax (i.e., concealed in groove between prothoracic shield and mesothoracic shield). MD1 a microseta on outer edge of fold, directly anterior to seta SD2, with apex in space between thoracic shield and adjacent mesothoracic shield; seta MSD1 a microseta on anterior slope of fold, slightly ventrad of seta MD1, with apex in space between microsetal fold and prothoracic shield; seta MSD2 directly posterior to seta MD1 on posterior declivity of

fold, with apex in space between microsetal fold and anterior mesothoracic shield. Setae MSD1 and MSD2 subequal in size, slightly smaller than seta MD1. Single SV seta in middle of large subventral, pale yellow shield; SV subequal or larger in size than setae D1 and SD2, but smaller than setae D2 and SV1. Two transverse plicae between mesothoracic coxae and posterior margin of prothorax; anterior plica very small, not visible in external ventral view, and bearing seta MV1 on its posterior face; posterior plica larger, visible in ventral view, bearing seta MV2 posterodorsal to seta MV3 on anterior declivity; MV2 directly opposite dorsal extremity of anterior margin of mesocoxa with apex extending forward and contacting posterior ventral region of prothorax. Setae MV1, MV2 and MD1 subequal in length; setae MSD1, MSD2, and MV3 subequal in length, slightly shorter than setae MV1, MV2, and MD1. Mesothoracic coxae separate at base. Subdorsal peg organ located in membrane on extreme anterior edge of posterior mesothoracic shield, opposite ventral posterior extremity of anterior mesothoracic shield, dorsoventrally midway between level of setae D2 and SD2. Mesothoracic leg as for prothorax, in general all setae slightly smaller, especially anterior coxal setae.

Metathorax (Fig. 4): As for mesothorax with the following differences; peg organ more exposed on leading edge of posterior metathoracic shield; anterior metathoracic shield slightly longer on midline than that shield on mesothorax; posterior metathoracic shield slightly shorter on midline than that shield on mesothorax; leg as on mesothorax.

Abdomen (Figs. 4-5): Generalized abdominal segment consisting of four annuli; first (anteriormost) annulus small, nearly hidden from view between second annulus and posterior edge of preceding segment, diminishing laterally to simple plica; second annulus largest, bearing seta D1; third annulus smaller than second, bearing seta



Figs. 4-5. Chaetotaxy of thoracic and abdominal segments of *Phassus* sp. (semischematic views). 4, Left side of thorax and first two abdominal segments. 5, Left side of abdominal segments 6-10. Symbols used: Ab1-2, Ab6-10, abdominal segments I, II, and VI through X; D1-D2, dorsal setae; L1-L3, lateral setae; LAa, lateral pore of Ab10; MD1, dorsal proprioceptor seta; MSD1-MSD2, subdorsal proprioceptor setae; MV1-MV3, ventral proprioceptor setae; PP1, paraprot seta; SD1-SD2, subdorsal setae; SV1-SV3, subventral setae; T1-T3, thoracic segments I to III; V1, ventral seta; XD1-XD2, anterior dorsal setae of T1; XDa-XDc, anterodorsal pores of T1.

D2; fourth annulus not sclerotized dorsally, subequal in size to third annulus.

Generalized setation of abdominal segments: Setae D1 and D2 subequal in size, similar in position to same setae on T3. D2 ventral to D1. Seta SD2 in center of large pale pinaculum, subequal in size to seta D1, about half size of seta SD1 on anterodorsal corner of same pinaculum. Peg organ conspicuous, dark, located in membrane midway between ventral side of plate D1 and

dorsal side of plate bearing setae SD1 and SD2.

Spiracle on first abdominal segment (Ab1) largest, subequal to spiracle on T1 (height 0.92 mm, length 0.42 mm), that on Ab8 smaller (height 0.81 mm, length 0.42 mm), that on A2 smaller still (height 0.78 mm, length 0.42 mm) and those on A3-A7 subequal and smallest (height 0.69 mm, length 0.42 mm).

Abdominal segment 1: Seta MD1 ante-

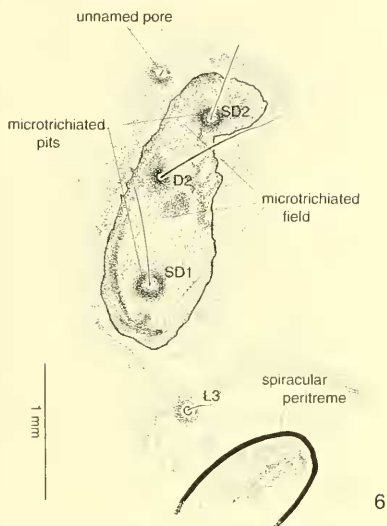


Fig. 6. Detail of microtrichiated field of larval prothorax, *Phasstus* sp. Symbols used: D2, dorsal seta; L3, lateral seta; SD1–SD2, subdorsal setae.

rior to peg organ, at bottom of groove between first and second annulus. Cuticle enfolded around seta MD1 forms open sub-spherical cavity, not collapsed by movement. Pinaculum of seta L2 directly posterior to spiracle; pinaculum of seta L1 dorsoposterior to pinaculum L2. Seta L3 slightly anterior to spiracle on extreme anterior edge of large longitudinal plate extending posterior to intersegmental groove. Setae SV1, SV3 located on dorsal half of same pale pinaculum.

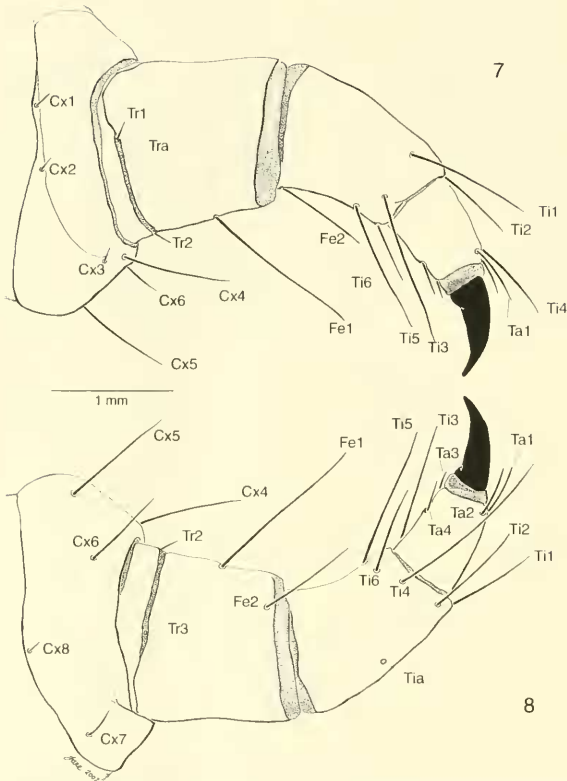
Abdominal segment 2: As for Ab1 with following differences: Seta MD1 located near bottom of groove between annulus 1 of Ab2 and annulus 4 of segment Ab1; large oval plate without setae on annulus 1 at level of spiracle, subequal in size to spiracle; seta SD2 on small pinaculum approximate and dorsal to larger pinaculum bearing SD1; seta L1 located on extreme dorsoposterior edge of plate bearing L2, not on separate plate; seta MV relatively large, more

than twice length of seta MV on segment Ab1.

Abdominal segments 3–6: As for segment Ab2 with following differences: seta SD2 on distinct pinaculum on segments Ab3–Ab4, that pinaculum reduced or absent on Ab5–Ab7; seta L1 on distinct small pinaculum posterodorsal to larger plate bearing seta L2; seta SV1 largest, most posterior, and dorsalmost of any SV seta; seta SV2 anteroventral to seta SV1 on same plate, half the length of SV1; seta SV3 anteroventral to SV2 on same plate, about half length of seta SV1; seta V1 directly between base of prolegs on same sclerotized plate encircling proleg and bearing all SV setae; seta MV3 directly anterior to proleg on extreme anterior edge of sclerite bearing setae V1 and SV1–SV3. Crochet conformation as uniordinal biserial ellipse, outer series with crochets greatly reduced in length.

Abdominal segment 7: As for segment Ab6 with following differences: setae SV1 and SV2 located on same plate, half the diameter of homologous plate on Ab2; seta SV3 absent; seta V1 directly ventral to seta SV2 on very small sclerotized plate; seta MV3 directly anterior of seta V1, subequal in size to seta MV3 on other abdominal segments.

Abdominal segment 8: As for segment Ab7 with following differences: spiracle subequal in size to that on segment Ab2; seta MD1 exposed in flat region anterior to annulus 1; seta SD1 on very small basal plate, SD2 anterodorsal to SD1, without sclerotized basal pinaculum; no prespiracular plate on annulus 1; seta L1 lacks pinaculum; plate around seta L2 smaller than adjacent spiracle; seta L3 located on small pinaculum anterior to and slightly separated from larger lateral plate without setae; setae SV1 and SV2 very close on shared basal pinaculum; seta V1 on small distinct plate; seta MV3 much smaller than same seta on segments Ab2–Ab7, near outer edge of intersegmental groove, halfway between SV1 and V1.



Figs. 7-8. Chaetotaxy of prothoracic leg of last instar larva of *Phassus* sp. 7. Anterior view of left prothoracic leg. 8. Posterior view of left prothoracic leg. Symbols used: Cx1-Cx8, coxal setae; FE1-FE2, femoral setae; MTRa, anterodorsal pore of trochanter; Ta1-Ta4, tarsal setae; Ti1-Ti6, tibial setae; Tia, posterodorsal pore of tibia; Tr1-Tr3, proprioceptor seta of trochanter.

Abdominal segment 9: As for segment Ab8 with following differences: only a single obvious annulus; all setae with reduced basal pinacula; D1 setae much closer to each other across midline than are setae D2 across midline; SD1 directly ventral to D1; seta SD2 missing; MD1 anterior to SD1, extending into intersegmental groove on anterior slope of segment; setae L1, L2, and L3 in vertical row, equidistant, directly ventral to D2; setae SV1 and SV2 as on seg-

ment Ab8, directly ventral to L3 but not on shared basal pinaculum; seta VI strong, near ventral midline; seta MV3 slightly ventral to SV2, enfolded within intersegmental groove.

Abdominal segment 10: Three setae (D1, D2, SD1) on dorsal anal shield; two setae (here interpreted as seta L1 (anterior) and paraproct seta PPI (posterior)) and one pore (LAA) on posterior plate; two setae below anus and dorsal to proleg (interpreted as se-

tae L2 (anterior) and L3 (posterior)); two lateral setae anterior to proleg (interpreted as setae SV1 (dorsal) and SV2 (ventral)); two ventral setae anterior to proleg (interpreted as seta V) (posterior near edge of planta) and nearly macrosetose MV3 (near intersegmental groove with segment Ab9). Crochet conformation triserial, uniordinal, arranged as two semicircular loops on each anal proleg.

PROBLEMS WITH HOMOLOGY AND SETAL NOMENCLATURE

The multiplicity of chaetotaxic systems for lepidopterous larvae, and in particular for hepialids, makes it difficult to recognize and name setae that are homologous at the ordinal level. Resolution of this problem is not possible in this paper and awaits more extensive research on setation in Exoporia, other basal clades of Lepidoptera, and Ditrysia. As an initial set of concerns for future research in this area, we provide an annotated list of the setal groups found to be problematic in this study.

1. Thoracic and abdominal setae of the MV and V groups of Hinton (1946). Confusion arises from variation in stereographic position of setae and their relative size and structure.

2. Setae of the SV group, especially on the abdomen. This is a classic dilemma in many ditrysiian superfamilies, especially for variation on the first two abdominal segments, and segments where prolegs may be reduced.

3. Setation of abdominal segment 10. This segment consists of problems of both number and position of setae on the anal shield (D and SD groups) and of presence and placement of setae on more ventral portions of the segment (L, SV, and V groups).

4. MD and MSD microsetae on thoracic segments. The problem here may be due to inadvertent but alternate nomenclature applied by Hardy (1973) and Yasuda and Abe (1986). We concur with Nielsen and Kristensen (1989).

5. Head setae. Many problems with al-

most every setal group on the head result from confusion about variable placement and size of setae. Although the chaetotaxy is not altered, a more thorough discussion of this problem is given below.

6. D, SD, and MXD group setae and associated pores on the prothorax. These are variable features unique to Exoporia. Prothoracic D and SD setae are discussed in detail below.

Setation of the head.—Investigators using setae in the comparative study of Lepidoptera larvae have usually followed prior convention in chaetotaxy. Students of hepialid larvae have revealed consistent differences in setal placement with ditrysiian larvae, and these have resulted in a number of nomenclatural systems, each differing slightly from the others. This is especially true for setae of the head where a system dating from Heinrich (1916), Gerasimov (1935) and Hinton (1946) was modified by Hasenfuss (1969) for Hepialidae and by Stehr (1987) for Ditrysia, then variously modified again for Hepialidae by Wagner (1987), Wagner et al. (1989), Leonard et al. (1992), and Nielsen and Kristensen (1989). To avoid confusion other workers have wisely followed the nomenclature of recent authors when comparing setae within Hepialidae (Dugdale 1994, Zilli 1998). No worker since Hasenfuss has proposed and adequately defended a chaetotaxic system that seeks to recognize homology across the entire order, as such an undertaking would require detailed study of all world lineages.

For some groups of cranial setae there is no controversy among published descriptions in the last fifty years. All workers agree on the naming of setae on the frontal and adfrontal sclerites, and concur that pore AFa is absent in hepialids. They further agree that there are two mandibular setae, but do not distinguish between them (the basal seta is here named M1, the distal seta M2). All workers agree on the number and placement of L-group setae, and of SS-group setae (sometimes labeled SO1–SO3

(subocellar setae) as opposed to SS1–SS3 (substemmatal setae)).

For other groups of cranial setae there are major differences in opinion as to nomenclature. These differences may be clarified by noting how various authors have treated each major group of setae. Treatment of clypeal setae is divided into two groups: 1) those naming the lateral setae C1 (Hinton 1946, Hasenfuss 1969, Nielsen and Kristensen 1989, Dugdale 1994), and 2) those naming the medial setae C1 (Wagner 1987) as in *Ditrysia* (Stehr 1987).

Treatment of labral setae is ignored by all workers, but all concur in their drawings that hepialids have five pairs of externally visible labral setae. We here call these LR1–LR5 with a single pore, LRa, following the nomenclature of Rawlins (1992) as applied to ditrypsian larvae. The homology of the lateral labral seta, LR5, with the ditrypsian condition is uncertain as there are two lateral setae on each side in that lineage, LR5 and LR6.

Numbering of stemmata in hepialids is not provided by any of these workers. The system followed here is consistent with that used for *Ditrysia*, assigning numbers for the left side of the head from 1 to 6 in a counter-clockwise direction such that the most ventral stemma near the posterior edge of the antennal fossa is 5.

Treatment of S-group setae is divided into three groups: 1) those following the ditrypsian system (Stehr 1987) and recognizing three S-group setae with S1 inside the stemmatal circle and S3 microsetose (Hasenfuss 1969), 2) those following the ditrypsian system but considering S3 to be absent, replaced by seta G2 or MG2 (Nielsen and Kristensen 1989, Dugdale 1994), and 3) those adopting a system with S1 anterior to the stemmatal region and adjacent to the anterior mandibular condyle, S2 within the stemmatal field, and S3 immediately posterior to the stemmata (Hinton 1946, Wagner 1987).

Treatment of the genal setae may be divided into two groups: 1) those using the

ditrypsian system (Stehr 1987) with a single genal seta and pore, MG1 and MGa (Hasenfuss 1969), and 2) those recognizing two genal setae and a pore, G1, Ga, and G2 (or MG1, MGa, and MG2) (Hinton 1946, Wagner 1987, Nielsen and Kristensen 1989, Dugdale 1994).

Treatment of the dorsal setae is also divided into two groups: 1) as in *Ditrysia* (Stehr 1987) with three dorsal setae and a pore (MD1–MD3 and MDa, or V1–V3 and Va) of which MD1 or V1 is macrosetose (Hasenfuss 1969, Nielsen and Kristensen 1989, Dugdale 1994), and 2) those recognizing two dorsal setae and a pore, all microsetose (MD2–MD3 and MDa, or V2–V3 and Va) (Hinton 1946, Wagner 1987).

All workers agree on naming P1 setae, but treatment of P2 setae is divided into three groups: 1) the ditrypsian condition with P2 posterodorsal to P1 and associated with pore Pb (Stehr 1987), 2) the ditrypsian condition with P2 posterodorsal to P1 but not associated with a pore Pb (Hinton 1946, Wagner 1987), and 3) with P2 lateral or lateroventral to P1 and associated with a pore Pb (Hasenfuss 1969, Nielsen and Kristensen 1989, Dugdale 1994).

All past treatments agree on recognition of seta A2, and the absence of pores Aa and Pa. Treatment of other A-group setae is controversial and may be divided into two groups: 1) those naming the anteriormost seta near the anterior articulation of the mandible as A1 with seta A3 near stemma 2 (the ditrypsian system (Stehr 1987) followed for *Hepialidae* (Hasenfuss 1969, Nielsen and Kristensen 1989, Dugdale 1994)), and 2) those naming the seta associated with stemma 2 as A1, and that associated with pore Pb as A3 (Hinton 1946, Wagner 1987).

Careful study of the bewildering situation above reveals that the fundamental conflict for determining setal homologies is between the size of setae (microsetose versus macrosetose) and their stereographic placement relative to each other and to pores. If the size of setae is ignored, then cranial se-

tae of Ditrysia and Hepialidae are spatially and numerically consistent with one exception: seta P2 in hepialids is displaced ventrally and laterally from the expected position in Ditrysia. This arrangement requires recognizing the ventral genal microseta in hepialids (MG2 of authors) as homologous with the posterior macroseta S3 of Ditrysia and treating the posterior dorsal macroseta of hepialids as homologous with the anterior dorsal microseta of Ditrysia (MD1 of authors). Under this system there is no need to violate consistent spatial associations of A-group or S-group setae as proposed by Hinton (1946) and Wagner (1987).

If the microsetose or macrosetose condition of setae is hypothesized to be so important that setae of different sizes cannot be considered homologous, then a diversity of ad hoc hypotheses on setal homology are required to account for all setae. This requires switching the nomenclature of seta A1 and S1, thereby changing their stereographic placement on the head capsule relative to the mandible and stemmata, increasing the number of genal microsetae from 1 to 2, decreasing the number of dorsal microsetae from 3 to 2, hypothesizing the complete disappearance of macroseta S3, associating seta A3 with pore Pb, or removing seta P2 from association with that pore, and so on.

Given that both ditrysiian and exoporian larvae possess the same number of primary cranial setae in very similar spatial relationship to each other and to cranial landmarks such as the antennal fossa, mandibular condyles, adfrontal sclerites, and stemmata, a parsimonious hypothesis of homology for these setae involves accepting major changes in setal size and a lateroventral shift in the position of seta P2. A chaetotaxic system corresponding to such homology requires application of names for macrosetae to microsetae (the hepialid seta MG2 becomes S3) or vice versa (the hepialid macroseta V1 become MD1). In respect it is unfortunate that a special nomenclature for microsetae arose following Hinton

(1946) as this may have obscured major evolutionary shifts in setal size and function, and in any event has greatly complicated hypotheses of homology with an already abstruse chaetotaxy. This paper is not the place to present a testable, homologous system of nomenclature for setae on larval Lepidoptera or other holometabolous larvae, but the above discussion should underscore the need to do so in order to more clearly understand the evolution of setal size, placement, and function.

Microtrichiated pits and fields.—Previous authors have used a variety of terms to describe regions of microtrichiated cuticle surrounding the base of setae in larval Lepidoptera, including "pocket" (Rawlins 1984), "pigmented sensory pit" (Wagner 1987), "microtrichiated pit" (Nielsen and Kristensen 1989), "pigmented pit with microtrichiated walls" (Rawlins 1992), "microtrichial bed" (Leonard et al. 1992), and "felted pits" (Dugdale 1994). These terms confuse two different cuticular features, both distinguished by the presence of microtrichiae: 1) a relatively small, deeply impressed pit surrounding the base of a single seta, and 2) a more extensive, concave or flat region that may enclose one or more setae. We limit the expression "microtrichiated pit" to the former condition, almost always in association with filiform tonosensilla, and use the expression "microtrichiated field" to describe the latter. Microtrichiated pits and fields often occur independently, but pits can also be located within fields as in *Phassus*, and may be developmentally related, differing only in degree of expression.

Prothoracic setae.—A distinctive, and possibly apomorphic feature of some hepialid larvae is the presence of three setae (D2, SD1, and SD2) enclosed by a single continuously microtrichiated field, as opposed to having the field divided into two separate regions, each enclosing a seta. Because these setae are ventrally displaced from the position D2 occupies in Ditrysia, there has been confusion over their homol-

ogy relative to other thoracic segments and prothoracic setae in other Lepidoptera. The problem is clarified but not resolved in the following paragraphs.

Criteria most often used to determine the homology of setae on a single larva may be broadly grouped into two categories: *Criterion 1*, stereographic position relative to other setae with respect to body axes (dorsal, ventral, anterior, posterior), and *Criterion 2*, morphological details of the seta itself (size, shape, color, surface microsculpture, and others) including region of articulation with adjacent cuticle. Analysis of homology for setae results from comparative study of their position and morphology between developmental instars and between larvae of different taxa. Ontogenetic comparisons are problematic, especially those involving first instars, as there is no a priori reason to believe that apomorphic features could not have evolved in the first instar. No first instar *Phassus* larvae were available for study.

To determine the homology of setae D2, SD1, and SD2 under the above criteria, we consider first the situation for each condition in Dityrsia.

Seta D2 *Criterion 1*: D2 dorsal and posterior to SD1 and SD2 (or at most with D2 directly dorsal to those setae).

Criterion 2: D2 variable in length, often shorter than SD2 and/or subequal in length to SD1; never positioned in a microtrichiated pit on any segment, and always a typical macroseta, never a filiform tonosensillum.

Seta SD1 *Criterion 1*: SD1 anterior and ventral to SD2, at most directly anterior or directly ventral to SD2 (never posterior or dorsal to SD2).

Criterion 2: SD1 shorter than SD2 in many lineages, but in some subequal or greater in length than SD2; positioned in a

microtrichiated pit in some lineages; a filiform tonosensillum in some groups.

Seta SD2 *Criterion 1*: as above.

Criterion 2: as above, not associated with microtrichiated pit and not a filiform tonosensillum.

Contrast the above pattern to that observed in *Phassus* using the terminology of Wagner (1987):

Criterion 1.—D2 is ventral and anterior to SD2, dorsal and posterior to SD1. Conclusion: *Placement of both D2 and SD2 violates stereographic conditions both dorsal-ventral and anterior-posterior*. Seta SD1, however, is in accordance with *Criterion 1* in the Dityrsia.

Criterion 2.—D2 slightly longer than SD1 and SD2 which are subequal in length; D2 a strong, typical tactile macroseta, but SD1 and SD2 are filiform tonosensilla positioned in microtrichiated pits; all three setae and pits within a microtrichiated field. Conclusion: D2 in accordance with *Criterion 2* (large macroseta without a microtrichiated pit); SD1 in accordance (tonosensillum with a microtrichiated pit); *SD2 not in agreement with Criterion 2 being a tonosensillum in a microtrichiated pit*.

Switching names for setae D2 and SD2 conforms to the nomenclature of Nielsen and Kristensen (1989) produces the following situation under *Criteria 1* and *2*.

Criterion 1.—All setae are in accord with the condition in Dityrsia.

Criterion 2.—D2 subequal in length to SD1 and shorter than SD2; SD2 a strong, typical tactile macroseta, but SD1 and D2 are filiform tonosensilla positioned in microtrichiated pits; all three setae and pits within a microtrichiated field. Conclusion: SD2 and SD1 in accordance with *Criterion 2*, but *D2 not in agreement with Criterion 2 being a tonosensillum in a microtrichiated pit*.

The above analysis of setal condition in

Phassus reveals a conflict with both Criterion 1 and Criterion 2. Resolution requires weighting one over the other. In this case, weighting Criterion 2 over Criterion 1 requires hypothesizing convergent development of complex morphological features (tonosensillum in a microtrichiated pit) for either seta SD2 (Wagner 1987) or seta D2 (Nielsen and Kristensen 1989). Weighting Criterion 1 over Criterion 2 requires hypothesizing shifts in spatial placement for setae D2 and SD2 under Wagner's terminology, but not under that of Nielsen and Kristensen (1989). It is tempting to conclude that the most parsimonious solution would be the latter system, but this requires development of D2 as a tonosensillum in a microtrichiated pit, a situation not encountered elsewhere in Lepidoptera. The alternative system (Wagner 1987) requires relatively slight shifts in stereographic position for two setae and development of SD2 as a tonosensillum, a condition we feel more likely than for D2 insofar as tonosensilla are usually SD group setae in other Lepidoptera.

It is important to realize that a testable determination of which criterion to emphasize is not possible without further morphological and comparative study. For the time being we prefer to accept slight shifts in setal position and tonosensillar morphology for SD2 as more likely than convergent development of tonosensillar morphology in D2. Favoring a chaetotaxic system emphasizing the greatest likelihood of homology, we have used the terminology of Wagner (1987) in agreement with the logic of Dugdale (1994). Resolution of this problem may result from comprehensive study of tonosensilla for all larval instars across Lepidoptera.

IMPLICATIONS FOR PHYLOGENY AND BIOGEOGRAPHY

The inclusion of D2 with SD1 and SD2 within a common microtrichiated field in *Phassus* supports a monophyletic relationship with the Asian/Australasian stem-bor-

ing Hepialidae with the exception of *Zelotypia* that is characterized by two separate microtrichiated areas for SD1 and SD2. Dugdale's (1994) reference to all three setae being included in *Zelotypia* appears to be incorrect (Dugdale 1999, pers. comm.). A further larval character that may support a close affinity between *Aenetus* and *Phassus* is the elongate shape of the pit L3a on the mesothorax and metathorax. This pit is slightly elongate in *Zelotypia* and *Endochlita*. The pit is round in larvae of the root stem boring *Phymatopus californicus* (Boisduval) of North America, and the detrital feeding *Dumbletonius unimaculata* (Salmon) (as *Trioxycaenus eysii* of authors) in New Zealand (Grehan et al. 1983). The presence and shape of pits have been overlooked in many larval descriptions but may provide significant phylogenetic characters. The anterior margin of the labrum of *Aenetus*, *Phassus*, and *Endochlita* is trilobate, a feature also recorded from *Sthenopis*, *Phymatopus*, *Zelotypia*, and *Leto* (Table 1). The larval description of *Cibyra seta* (Schaus) by Rojas de Hernández and Chacón de Ulloa (1982) illustrates a prothoracic microtrichiated field common to SD1 and SD2 that excludes D2. Larval descriptions of the South American wood-borer *Trichophassus* are insufficient to confirm a trisetose setal pit, and the adult male of *Trichophassus giganteus* lacks metatibial androconia (Briquet 1956). Kristensen (1998) notes that metatibial androconia have evolved several times in Lepidoptera. Androconia of *Oncopera* and *Pteromytrans* may have originated separately from those of the wood-borer lineages since the scales of *Aenetus*, *Endochlita* and *Phassus* are pale reddish brown or orange brown in contrast to the gray brown androconia of *Oncopera* and *Pteromytrans* (Table 1). At least one species of *Aenetus* lacks metatibial androconia (Wagner and Rosovsky 1991).

Kristensen's (1998) suggestion for a close relationship between the monotypic wood-boring genus *Leto* of South Africa and the Australasian *Aenetus* was based on

biogeographic speculations and is not otherwise substantiated (Kristensen pers. comm., 1999). Metatibial androconia are absent from *Leto venus* (Cramer) and larvae have no microtrichiated fields at the base of SD1, SD2, or D2. Although larvae of *L. venus* are wood-borers, callus feeding is not recorded and pupae reside in a unique tubular silk/frass extension of the tunnel beyond the bark surface (Peabody Museum of Natural History specimens). We conclude the genera *Phassus*, *Endoclita*, and *Aenetus* represent a monophyletic lineage in reference to the trisetose pit, with the possibility that *Zelotypia* and *Cibyra* are more distantly related, and possibly comprising a monophyletic lineage of callus feeders and wood-borers along with the *Phymatopus*-clade within the Hepialidae sensu stricto.

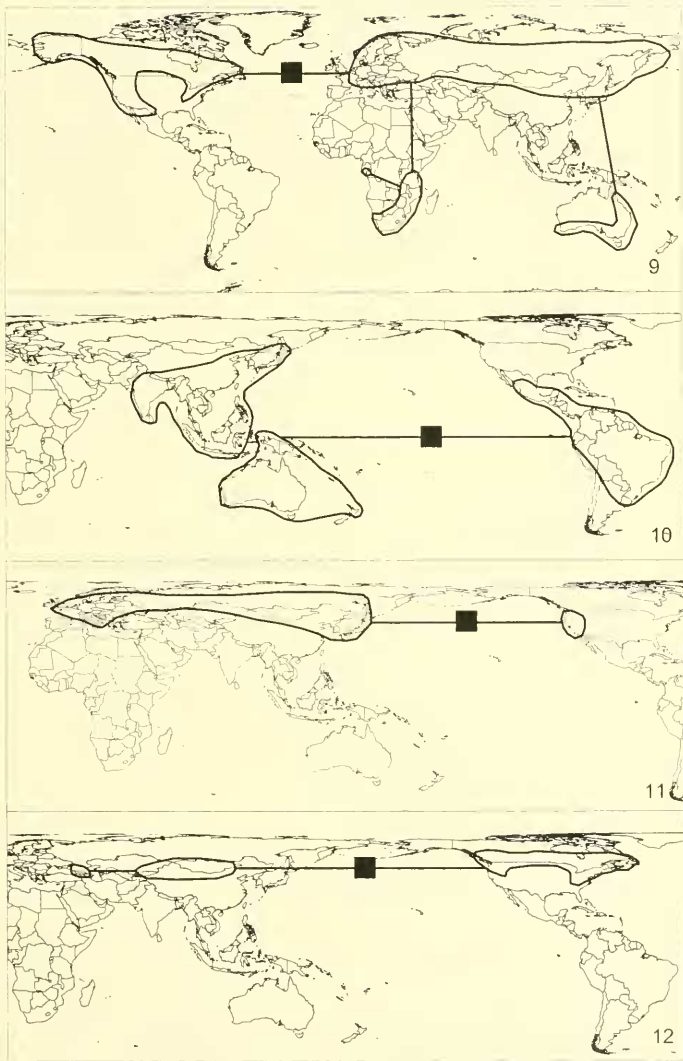
Exoporian and hepialid lineages are predicted by Nielsen et al. (2000: 832) to be 'very much' older than the fragmentation of Gondwana. The oldest fossil record for hepialoids are Paleocene Europe, mid-Miocene China (Kristensen and Skalski 1999) and Eocene New Zealand, the latter being fossil wing scales that may be referable to the extant genus *Wiseana* Viette (Evans 1931, Harris 1984). A purported Upper Cretaceous amber mnesarchaeid wing is considered by Kristensen and Skalski (1999) to be unsubstantiated in the absence of "strong family autapomorphies" in the specimen. In the absence of a well-endowed fossil record, Holloway and Nielsen (1999)

regard the age of Mesozoic events influencing distribution patterns within Lepidoptera to be an open question. Grimaldi's (1999) interpretation of fossil evidence proposed an Upper Jurassic origin for tongued Lepidoptera (Glossata) and a Cretaceous origin for basal glossatan families (including Hepialidae). Grehan (1991) suggested the biogeographic patterns of Lepidoptera and Angiospermae support a pre-Cretaceous origin for lepidopteran lineages to family level. Lack of evidence for discrete continental monophyletic exoporian faunas is contrasted by Nielsen et al. (2000:832) with their "temptation" to view the Exoporia as relicts of Gondwanic fragmentation and resulting isolation and speciation.

Most Mesozoic models of evolution are linked to the geological fragmentation models of Pangaea or its Gondwanic and Laurasian fragments (Craw 1982). Distribution patterns congruent with this history are expected to exhibit distributional and phylogenetic links across the Atlantic and Indian Oceans resulting from the breakup of ancestral distributions on the supercontinents of Gondwana and Laurasia. This historical model is consistent with the distributions of primitive hepialid lineages (Fig. 9) comprising a biogeographic track connecting Australia, Africa, North America, and Eurasia (this connection does not assume a monophyletic status for these genera). In contrast, the *EndoclitalAenetus/Phassus* clade is absent from Africa, although pres-

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Figs. 9–12. 9. Biogeography of 'primitive' Hepialidae. A minimal spanning link connects the generalized distributions of the African *Afrotheora* and *Antihepialus* with *Fraus* across the Indian Ocean basins (with baseline of track denoted by solid square) with an additional link to *Gazoryctra* between the African genera and the North American and Eurasian *Gazoryctra*. This pattern may be compatible with conventional 'Pangaean' origin although the genera are currently not known to be monophyletic (distribution data from Holloway and Nielsen 1999: Fig. 21–22). 10. Pacific biogeography of *Endoclita*, *Aenetus*, and *Phassus*. The nearest neighbor criterion links the distributions of *Aenetus* (Australasia) and *Endoclita* (India-eastern Asia) with the American *Phassus* across the Pacific (baseline as a solid square). This spatial homology suggests the evolution of this lineage is more closely linked to the geological history of the Pacific basin than with the Atlantic or Indian oceans of Gondwana (distribution data from Grehan 1987, Nielsen and Robinson 1983). 11. Pacific interpretation for the distribution of *Phymatopus*-clade. Although the North American '*Phymatopus*' is in closest geographic proximity to the related European *Phymatopus* directly across the Atlantic, the western distribution of '*Phymatopus*' may be the result of a former trans-Pacific connection through extinction of Asian representatives as indicated here



by a north Pacific track and baseline (distribution data from Wagner 1985). 12, Pacific interpretation for the distribution of the *Sthenopis-Zenophassus* clade. As with the *Phymatopus* group, the Old World-New World disjunction between *Sthenopis* and *Zenophassus* may lie across the Pacific rather than Atlantic Ocean basins (distribution data from Tindale 1941—including Chinese records of '*Sthenopis*' auctororum nec Packard [1865] of uncertain status (Nielsen et al. 2000)).

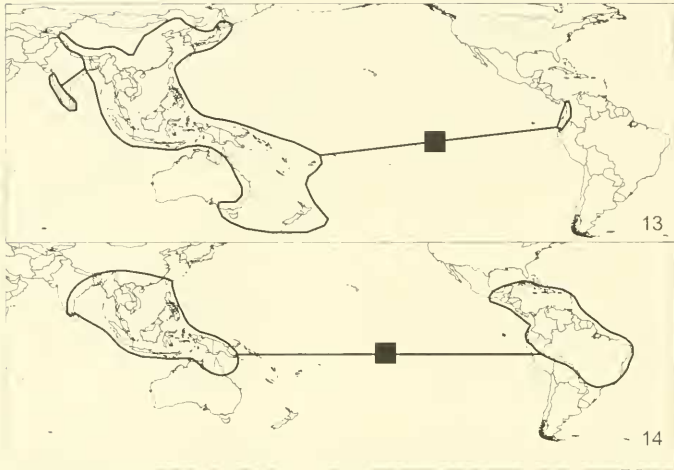


Fig. 13–14. Pacific spatial patterns. 13, Track for perichaetine earthworms (compiled from Easton 1987). 14, Track for the fabaceous genus *Ormosia* (from Croizat 1976, Fig. 1).

ent in the Gondwanic fragments of India, Australasia, and South America (Fig. 10).

A Gondwanic history for wood-boring Hepialidae may be supported by a close phylogenetic relationship being established with an African group such as *Leto* (Grehan 1984). Alternatively, the African gap may be accounted for by extinction of Gondwanic members or a biogeographic history for wood-boring and callus-feeding Hepialidae that bypasses Africa altogether. Gondwanic distributions bypassing Africa include tracks connecting Central and North America with the Mediterranean and Indian Ocean via the Tethyan geosyncline (Croizat 1964). Absence of wood-boring Hepialidae from North Africa and Europe does not support this biogeographic history. Distribution of the *Endochlita/Aenetus/Phassus* group is, however, consistent with Africa being 'bypassed' by a non-Gondwanic origin involving the Pacific Basin. This biogeographic connection may also be applicable to the *Phymatopus*-clade (Fig. 11) and to *Sthenopis/Zenophassus* (Fig. 12). There are also similarities in the geographic rang-

es of *Aenetus/Endochlita* with other Pacific groups such as the perichaetine earthworms (Fig. 13) in the Old World (Easton 1987) and the angiosperm genus *Ormosia* Jackson (Fig. 14) in both Old and New Worlds (Croizat 1976, fig. 1).

The geological evolution of the Pacific is a controversial biogeographic and geological subject. Geohistorical reconstructions treating the Pacific as a permanent oceanic basin are contradicted by the extensive documentation of allochthonous terranes around the Pacific Rim and Tethyan geosyncline. These terranes are widely interpreted as fragments of former Mesozoic and Tertiary island arcs or microcontinents of Pacific origin (Craw et al. 1999, Grehan 2001). Geological efforts to resolve the historical relationships between the circum-Pacific terranes include proposals for disruption of Mesozoic microcontinental fragments (e.g., Nur and Ben-Avraham 1977, 1989), fragmentation of oceanic superplume magmas (Kimura et al. 1994), and former island-arc bounded plates (Moore 1998). Pacific distributions comprise a bio-

geographic element distinct from Gondwanian or Laurasian distributions spanning the Indian Ocean and Pacific basins (Croizat 1958, 1976) and current biogeographic studies continue to verify a distinct Pacific pattern of biogeography for groups ranging from cycads and conifers (Contreras-Medina et al. 1999) to angiosperms (Heads 1999), dragonflies (De Marmels 2000), and dinosaurs (Rieppel 1999). A Pacific biogeographic homology for the origin of an *Endoclitia/Aenetus/Phassus* lineage, possibly along with other Hepialidae, provides a historical solution to the absence of *Exoporia* from West Africa (except for the marginal presence of *Antihepialus* in western Congo/Zaire) and Madagascar described by Nielsen et al. (2000: 831) as "extraordinary and inexplicable." Absence of taxa from West Africa and Madagascar, far from extraordinary, is commonplace with many such groups being Pacific in origin whereas West Africa and Madagascar are regions central to the Atlantic and Indian Ocean biogeographic patterns of Gondwana (Croizat 1952, 1958, 1968a–b). The Pacific homology proposed here for wood-boring Hepialidae corroborates the caution expressed by Nielsen et al. (2000) against interpreting distribution of *Exoporia* as relicts of Gondwanic fragmentation. The lack of exoporian monophyly within continents (Nielsen et al. 2000) may be the result of ancestral differentiation predating geological dissolution of both Pacific and Gondwanic regions.

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